S3: ODD

Supplement to:

Intraspecific trait variation in personality-related movement behaviour promotes co-existence.

CONTENT

BASIC PRINCIPLES[1]

Our movement model integrates a modified version of a memory-based movement model (Van Moorter *et al.*, 2009) and behavioural reaction norms (BRN, Dingemanse *et al.*, 2010) to explore the emergence of realistic home ranges in a community of species. These two elements of our model are introduced in the following sections as a basis for the subsequent Overview, Design Concepts and Details (ODD, Grimm *et al.*, 2006, 2010; Railsback and Grimm, 2019).

Behaviour reaction norms (BRN)

The BRN (Dingemanse *et al.*, 2010) formalizes behaviour as a relationship between an environmental gradient and the behavioural phenotype. In our model, the behavioural phenotype is the persistence of direction (PoD) and the environmental gradient is the strength of the perceived utility of memorized patches (*memory feedback*). PoD determines the magnitude by which the memory of resource locations (*patches*) affects the movement direction. The higher PoD, the more an animal turns towards known resource locations.

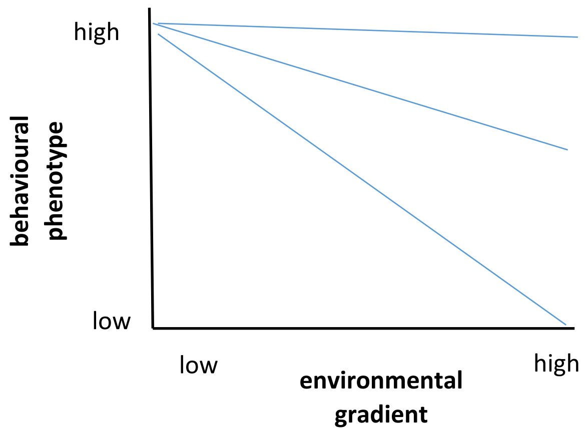


Figure 1. Behavioural reaction norm (BRN, Dingemanse *et al.*, 2010) that formalizes the relationship between behavioural phenotypes along an environmental gradient. In our study PoD is the behavioural phenotype and the memory feedback is the environmental gradient as perceived by the individual. Different behaviour types lead to different phenotypic behaviours under common environmental conditions as indicated by the three different linear relationships.

The BRN is modelled as a linear relationship that consists of two elements – the average behavioural expression (e.g. animal personality) and responsiveness (e.g. reversible plasticity) that are both defined by one parameter α. Different α-levels define different behaviour types (BTs). This assumed correlation between these two dimensions of behaviour is backed by empirical evidence (Natarajan *et al.*, 2009; Mazza *et al.*, 2018) and eases the subsequent analysis. The BRN is defined as:

$$PoD = 1 - \alpha * \mathrm{MemoryFeedback}$$

We categorize the BTs along a slow-fast-continuum *sensu* Réale *et al.* (2010). Animals with a higher α-level have a higher tendency to rely on their memory and we, hence, define them as shy, responsive

[1] We present these principles first, as they are essential understand the rationale and design of the entire model.

and thorough explorers. Animals that rather persist in their current movement direction are thought to be bolder, less responsive and superficial explorers (low α-level). We refer to BT as a behavioural trait and, hence, call the intraspecific variation around a mean BT intraspecific trait variation (ITV).

Memory-based movement

In the approach of Van Moorter *et al* (2009), animals' decision-making is based on the perceived utility of memorized patches. The perceived utility is the product of reference memory, the working memory and the maximum utility of a patch divided by the distance to that patch. Essentially, the reference memory decays over time mimicking forgetting, whereas the working memory increases hindering the animal to visit a patch that was already recently exploited. The maximum utility is the highest utility value an animal has encountered for a specific patch. Our approach differs slightly from Van Moorter *et al*. (2009) as the maximum utility (resource) can only be {0, 1}. Thereby the product of working memory, reference memory and maximum utility and, hence, the perceived utility would be zero for patches that did not have a resource. Hence, patches with resource 0 do not become part of the memory and the maximum utility as a state variable becomes redundant as it is always 1. Furthermore, the calculation of reference and working memory differs slightly which leads to a difference in parameter settings between our model and the algorithm by Van Moorter et al. (2009) that would lead to the same outcome (for details, see the submodels section below).

In the next step, the perceived utilities are multiplied with the unit vectors of the directions towards the memorized patches to generate attraction vectors. The mean attraction vector is the sum of all attraction vectors. The mean new heading of the animal is a compromise of the current heading and the mean attraction vector. The persistence of direction (PoD) defines the degree to which the animal remains directed towards its current heading.

Van Moorter *et al.* (2009) add stochasticity with a scale parameter based on the length of the mean attraction vector to represent decision uncertainty. Here we chose a different approach and used the length of the mean attraction vector as the environmental gradient and PoD as the behavioural phenotype *sensu* Dingemanse et al. (2010) to allow for plastic behaviour and fixed the scale parameter to a certain value. By implementing different relationships between phenotypic behaviour and environmental behaviour via different α-levels, a slow-fast continuum of BTs is generated.

OVERVIEW, DESIGN CONCEPTS AND DETAILS (ODD)

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based and other computational models (Grimm et al., 2006, 2010; Railsback and Grimm, 2019).

1 Purpose

The purpose of our model is to analyse the effect of personality-dependent movement behaviour on interspecific differences in competitive ability in foraging and coviability (Jeltsch *et al.*, 2019) and, implicitly, coexistence. The model aims at identifying the role of inter- and intraspecific variations in memory-based movement behaviour for coexistence in multispecies communities. We use the individuals' ability to obtain a certain amount of resources within a certain time frame as a proxy for competitive ability that provides, at the community level, an indicator for coexistence. To consider our generic model realistic enough for its purpose, we linked the emergent movement patterns to home ranges observed in a community of small, ground-dwelling rodents (Schirmer *et al.*, 2019).

2 State variables and scales

Entities included in the model are **Patches** and **Animals**.

Patches are square grid cells characterized by their coordinates and the boolean variable resource {0,1} and the boolean variable fertile {0,1}.

Rationale: The value of resource changes from 1 to 0 when visited by animals, whereas fertile remains constant for the whole simulation. Patches with fertile 1 and resource 0 change to resource 1 with a certain probability.

The distribution of fertile and resource is defined by two continuous parameters. Patchiness [0-100 %], which defines habitat heterogeneity, and resource-cover [0-100 %], which is the proportion of patches which are fertile 1. Via set-this-seed, landscape generation can be made reproducible by setting a seed for the random number generator. Low levels of patchiness translate to homogeneous landscapes with random resource distribution and high levels of patchiness translate to heterogeneous landscapes with patchy resource distributions.

Animals are characterized by: parameters alpha ([0, 1]) and the species-specific species-ID ([1 – 2]). Alpha specifies the relationship between the behavioural phenotype PoD (persistence of direction) and the memory-feedback, which specifies how the experienced environment affects movement. Alpha, hence, is the behaviour type (BT) with low values leading to unresponsive, bold, and superficial exploration and high values inducing responsive, shy, and through exploration. The species-specific means alpha is set by the parameters species-1-mean and species-2-mean.

The memory of an animal includes a list of memorized patches (mem-patch), a list of the time (mem-time) since the last visit of a memorized patch, and the number of resources gathered within 1,000 ticks (mem-resources) after a spin-up phase. The utility of elements of mem-patch determined by mem-time and the respective distance constitutes the length of the mean attraction vector (mem-feedback) which represents the environmental gradient of the behavioural reaction norm (BRN; Fig. 1).

Rationale: Animals are assumed to adapt their home ranging behaviour based on their expectations of the availability of resources. Behavioural changes require an environmental gradient to adapt to. In our model, the environmental gradient is defined by the perceived utility and location of memorized patches with resources. Utility and location constitute the length of the mean attraction towards memorized patches which together define the mem-feedback. This feedback increases with the total perceived utility of all patches and the more uniform the direction towards the patches is. The higher the feedback the more an animal expects to gain benefits from returning to memorized patches. Therefore, higher feedback is linked to a higher reliance on memory and, hence, lower the persistence of direction, PoD (details in section 7).

The boolean parameter population-dynamics defines whether **animals** starve and reproduce. The Boolean state variable breeds defines whether an animal is currently breeding and the continuous variable breeding-stage [0, 3600] defines the stage of the breeding process.

Rationale: Ecologically breeding-stage includes the time from conception to the point where offspring can acquire own resources for the first time. Offspring is only added to the simulation at the end of the breeding process, before its only abstractly represented by an increase in the energetic demand.

Since this is a generic model, the spatiotemporal resolution is not specified, but a single **patch** should represent a site where a foraging animal finds and exploits resources, i.e. it is specific enough to be distinguished from its surroundings and to be memorized. Accordingly, a time step corresponds to the time to move to and to exploit a **patch** that has a resource. The **spatial extent** of the landscape is 250 x 250 patches. The extent of the **temporal scale** is 2,000 time steps for analysing foraging efficiency and 200,000 time steps a coviability analysis. When analysing foraging efficiency, the first 1,000 time steps are used for initializing the individuals’ memories and resource competition dynamics.

Rationale: We chose the extent of the temporal scale to allow for a spin-up phase of the memory algorithm and to sample enough independent, so informative, relocations to analyse the individual home ranging behaviour. We chose the spatial scale to allow for emergent home ranges in a community.

3 Process overview and scheduling

In each time step, submodels are performed in the order given below, but the order by which the entities (**animals, patches**) perform their tasks changes randomly in each time step. The first 1,000 ticks are reserved for initializing the model, so no output is generated during this time. The submodels are described in detail in ODD section 7. The sequence starts with the submodels for the **animals**; in the following, bold and underlined fonts indicate names of submodels, while underlined ones refer to variables.

The submodel **get-memory-heading** calculates a mean heading towards memorized patches (mem-patch) based on a respective perceived utility that is a function of mem-time and the distance to members of mem-patch. The submodel **get-PoD** returns the current PoD based on the individual's alpha and the recent feedback from memorized locations (mem-feedback). The submodel **set-new-heading-and-move** returns the new heading as a compromise of the outputs of **get-memory-heading**, **get-PoD**, and noise added by a random value sampled from the van-Mises distribution with the scale parameter $\boldsymbol{\kappa}$ fixed to 10. The animal moves 1 spatial unit in the direction of the new heading.

Rationale: The lower the total perceived utility of patches and the lower alpha, the higher the PoD. The higher the PoD, the less the new heading changes towards the mean heading of memorized patches and the more the current heading remains.

If no patches have been memorized yet, **get-memory-heading** and **get-PoD** are skipped which leads to a correlated random walk determined by the van-Mises distribution.

Depending on whether the animal is on a patch with resource 1 or 0 and whether this patch is an element of mem-patch, different parts of the memory (mem-time, mem-patch, mem-resources) are updated via the **update-memory** submodel. If the resource of the patch is 1, its resource is set to 0. After the initial spin-up phase of 1,000 ticks, gathered resources are counted via mem-resources to calculate the foraging efficiency which serves as a proxy for competitive ability and, more indirectly, as a proxy for fitness.

If the parameter population-dynamics is true, the submodels **do-energetics**, **attempt-breeding**, and **create-offspring** are activated.

The submodel **do-energetics** regulates maintenance costs by reducing the value of mem-resources. If breeds is true, also breeding costs are imposed. If mem-resources drops below zero, the animal dies.

If breeds is false, the **attempt-breeding** submodel is executed. Here, the animal attempts breeding whereas the likelihood to engage breeding depends on the level of mem-resources. The higher mem-resources, the more likely the animal will switch breeds to true.

If the **breeding-stage** is at its maximum, the animal generates five offspring that share the same species-specific traits (species-mean, species-ID) and are assigned a value of alpha that is sampled from the species-specific uniform distribution defined by species-mean and ITV.

If population-dynamics is true and if there are less than two different species left, **save-output** is executed.

After all animals performed the previous submodels, patches with resource 0 and fertile 1 perform the submodel **grow-resources** to reset resource from 0 to 1 with a 1-% chance.

Finally, output is saved. If max-output is true, after the spin-up phase, each tick several observations (e.g. animal location, landscape settings, mem-resources) are written to a .csv-file in the submodel **save-output**. If max-output is false, **save-output** is only performed at the end of the simulation.

4 Design concepts

We took the following design concepts into account:

- Emergence. The movement behaviour emerges from the memory-based movement decisions. The foraging efficiency emerges from the adaptive decision-making, landscape structure, and the indirect interaction between the animals.
- Adaptation. Memory-based movement coupled with BRN leads to an adaptive movement behaviour, e.g. via an increase of home range sizes in landscapes of lower resource abundance.
- Learning. The home ranges tend to stabilize over time as animals learn about the position of fertile patches.
- Prediction. Animals implicitly predict that patches that they (again) visited but had/had no resources will also be favourable/not be favourable in the future.
- Sensing. Animals localize their current position and know the length and direction of the shortest path that connects them with memorized resource locations as well as they know the time since each memorized location was visited.
- Memory. Animals memorize patches with resource 1. Memory affects the decision-making as it constitutes an animal’s knowledge about the state of the environmental gradient and defines

the movement path. Furthermore, animals memorize when they exploited resources from a patch.

- **Interaction.** Indirect competition via shared resources affects an animal's memory and learning. Competitors may exploit resources in patches, which are perceived to be highly favourable as the probability of regrowth. Animals, therefore, affect each other's movement and hence home ranges.
- **Stochasticity.** The initial landscape and the community can be set up randomly. Memory-based movement is randomized by sampling from a van-Mises-distribution. The growth of resources is stochastic. All this stochasticity is used to represent variation caused by factors which are not represented mechanistically in the model.
- **Observation.** The foraging efficiency is the value of mem-resources divided by the number of recorded time steps. In the default setup, the last 1,000 time steps of the simulation were recorded. Optionally, relocations are tracked.

5 Initialization

The submodel **create-landscape** initializes the landscape by distributing resources and fertile to **patches** according to the settings by the continuous parameters patchiness [0, 100] and resource-cover [0, 100]. This random landscape generation can be replicated by setting a seed for the random number generator using the discrete set-this-seed input parameter [0, 100].

Afterwards, the submodel **spawn-animals** adds n-inds animals equally divided into n-species species (and hence different species-ID) to the landscape with random initial xy-coordinates. The distribution of behaviour types is defined by ITV and n-species, species-1-mean and species-2-mean. If n-species Is 1, the parameter species-1-mean defines the mean behaviour type of that species. If n-species is 2, species-2-mean additionally defines the mean behaviour type of the second species. The initialization consists of the submodels that are more precisely explained in the following:

create-landscape

The submodel **create-landscape** initializes the landscape by distributing resources and fertile to patches according to the settings by the continuous parameters patchiness and resource-cover. So, patchiness multiplied with resource-cover is the initial proportion of randomly chosen patches that have resource 1 and fertile 1. Around these patches, patches with resource 1 and fertile 1 are added until a proportion of patches with resource 1 equal to resource-cover is present. This random landscape generation can be replicated for a certain combination of patchiness and resource-cover by setting a seed using the discrete set-this-seed input parameter [0, 100]. Values from 1 to 100 refer to different seed of the random number generator. If set-this-seed is 0, no seed is set and the landscape generation is not reproducible.

fertilize

Subsubmodel of the **create-landscape** submodel. The variables resource and fertile of a patch are set to 1.

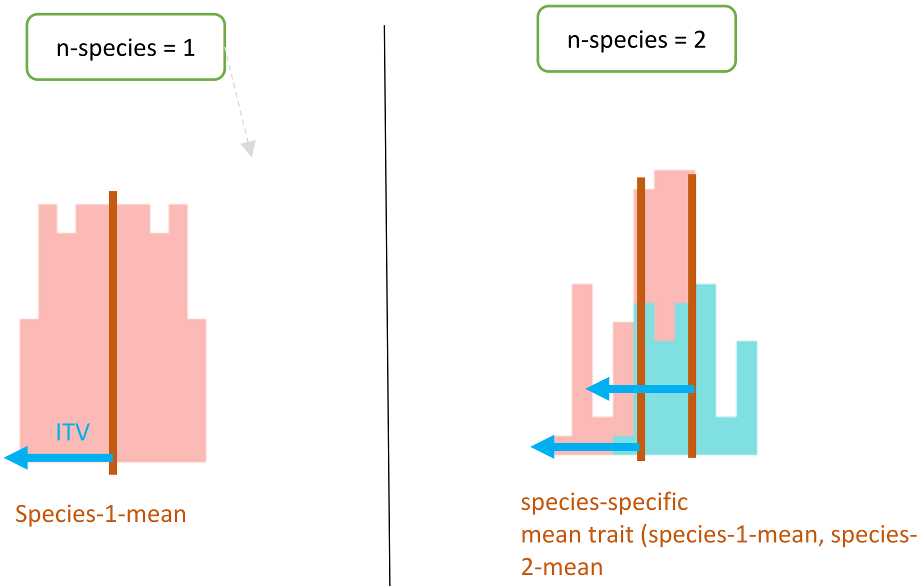
spawn-animals

Spawn-animals creates n-inds animals divided into n-species species with their individual properties. The distribution of the individual behaviour type (alpha) is defined by n-species. In any case, alpha is confined to the range of [0, 1].

n-species 1: An equidistant sequence of behaviour types from the minimum (species-1-mean – ITV) to the maximum (species-1-mean + ITV) with a length equal to the number of animals per species is generated. Minimum and maximum are set to zero or one, respectively, if they are outside the possible range of behaviour types [0,1]. For each species, individuals have a unique alpha value assigned from this sequence. This is repeated for each species.
Rationale: This mode is used to check the relationship of explicitly specified distributions of behaviour types on foraging efficiency at certain population densities and landscapes in single species simulations.

n-species 2: With two species, the mean alpha of one species is set by species-1-mean and of the other by speces-2-mean [0.25, 0.75]. There is an equal number of individuals per species. The individual alpha is sampled from a uniform distribution with the species-specific mean as the centre and ITV as the extent in the positive and negative direction. So, the minimum alpha of a species is species-specific mean – ITV and the maximum is species-specific mean + ITV. The assignment of species-specific mean alpha can be made reproducible if set-this-seed is set to a fixed value greater zero.

All state variables related to memory (mem-feedback, mem-time, mem-patch, mem-resources) are empty or zero, respectively. Only if population-dynamics is true, the level of mem-resources is set to 10 to prevent immediate starvation due to maintenance costs.



- Only intraspecific variation determined by ITV
- Mean trait defined by the global parameter species-1-mean
- Equidistant sampling of behaviour types
- Used for latin hypercube analysis, trait-foraging efficiency relationships

- Inter- and intraspecific variation
- Mean trait is species-specific and sampled from a uniform distribution ([0.25, 0.75])
- Random sampling of behaviour types from the species-specific uniform distribution characterized by ITV and the sampled mean trait
- Used for community analysis

6 Input data

There is no external input of data.

7 Submodels

Equations specified below are numbered ("Model equation I"). To link the ODD to the program implementing the model, and the code corresponding to each equation is marked, via comments, by the same label (e.g., "Model equation I") in the NetLogo program.

Table 1 Model parameters.

Entities	Parameter range	Description
Landscape (patches)		
patchiness	0 – 100 [%]	heterogeneity and amount of distributed resources
resource-cover	0 – 100 [%]	
max-pxcor	250 [const.]	size of x-dimension

max-pycor	250 [const.]	size of y-dimension
Set-this-seed	0 – 100	set seed for the random number generator during landscape generation
Community (animals)		
species-1-mean	0.0 – 1.0 [continuous]	mean behaviour type, species 1
species-2-mean	0.0 – 1.0 [continuous]	mean behaviour type, species 2
n-species	1 – 2 [n]	number of species
n-inds	1 – 750 [n]	number of individuals
ITV	0.0 – 1.0 [continuous]	one-sided width of the uniform behaviour type distribution
Movement algorithm		
rvm-kappa	10 [const.]	scale parameter of the van-Mises distribution (close to 0: uniform, more random. high values: normal, more correlated)
rate-mem-ref	0.99 [const.]	decay of reference memory
rate-mem-work	0.999 [const.]	decay rate of working memory
Miscellaneous		
Max-output	true, false	Give continuous model output
Max-ticks	2000, 100,000	Number of simulation steps
Population-dynamics	true, false	Enable population dynamics
Subfolder	string	Output folder
Population dynamics (only used if population dynamics is set to true)		
Breeding-cost	0.0075 [const.]	Increase in breeding cost per 100 time steps
Breeding-duration	3600 [const.]	Amount of time steps from conception to generating offspring
Litter-size	5 [const]	Amount of generated offspring
Maintenance-cost	0.18 [const]	Energetic costs per time step

get-memory-heading

Following Van Moorter *et al* (2009), the utility of the memory of a given location is a function of temporal and geographical distance. Hence, each memory of a location consists of spatiotemporal information given by mem-time and mem-patch. For a certain memory item i of an animal, the position of the respective patch (p_i) (mem-patch) and the time since the last visit (t_i) (mem-time) are used to calculate the perceived utility U_i. The shortest path $\overrightarrow{ap}$ between the current position of an animal (a) and p (on a torus, since we use wrapped boundaries) and its length $(|\overrightarrow{ap}|)$ are calculated. U_i is the product of the decay functions of the working memory (w) and the reference memory (r) with their respective decay rates (d_r) and (d_w) (0.99 and 0.999 as default values) divided by $|\overrightarrow{ap}|$.

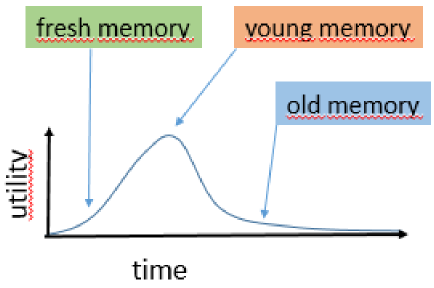


Figure 2 The perceived utility as the product of working memory and reference memory assuming the same geographical distance

Rationale: Choosing the values for d_r and d_w might appear arbitrary. In this rationale we reflect why we chose these parameters via some equations which are not part of the model.

The absence of competition and forgetting, an optimal perceived utility of a patch should, at constant geographical distance, only be a function of the likelihood that a resource regrew (R). R is a function of the time (t) since a patch has been exploited and the probability of resource growth per time step:

$$R(t, p_r) = 1 - (1 - p_r)^t$$

Competition, as the likelihood that a competitor exploits a known resource patch in the meantime, can be described as a function of the likelihood of regrowth (Fig. 4) and the likelihood of a competitor visiting a patch. The likelihood of regrowth per time step (p_r) and the likelihood that a competitor visits a patch (p_c) define the likelihood over time that a competitor exploits a given resource first:

$$C(t, p_r, p_c) = R * (1 - (1 - p_c)^t)$$

The difference between R and C is the residual likelihood that there is a resource at a certain a patch and a competitor has not exploited it first. This difference could be assumed to be the optimal perceived utility (if not regarding geographical distance to this resource). This optimal perceived utility is hump-shaped at different levels of competition and, thus, reasons the choses parameterization of the memory algorithm via (d_r) and (d_w) even without considering elements such additional as forgetting about the utility of patches. As a side note: one can infer from this observation that at higher levels of competition the penalty from an earlier forgetting about patches is reduced as the optimal perceived utility starts to decrease earlier.

The level of competition is likely to vary strongly between patches and individuals, so we cannot infer from these reflections to the actual likelihood that a competitor exploits a resource first. We decided to parameterize the memory algorithm to reach the highest perceived utility after around 100 ticks, which leads to a similar shape as the delta between the likelihood of competition and regrowth.

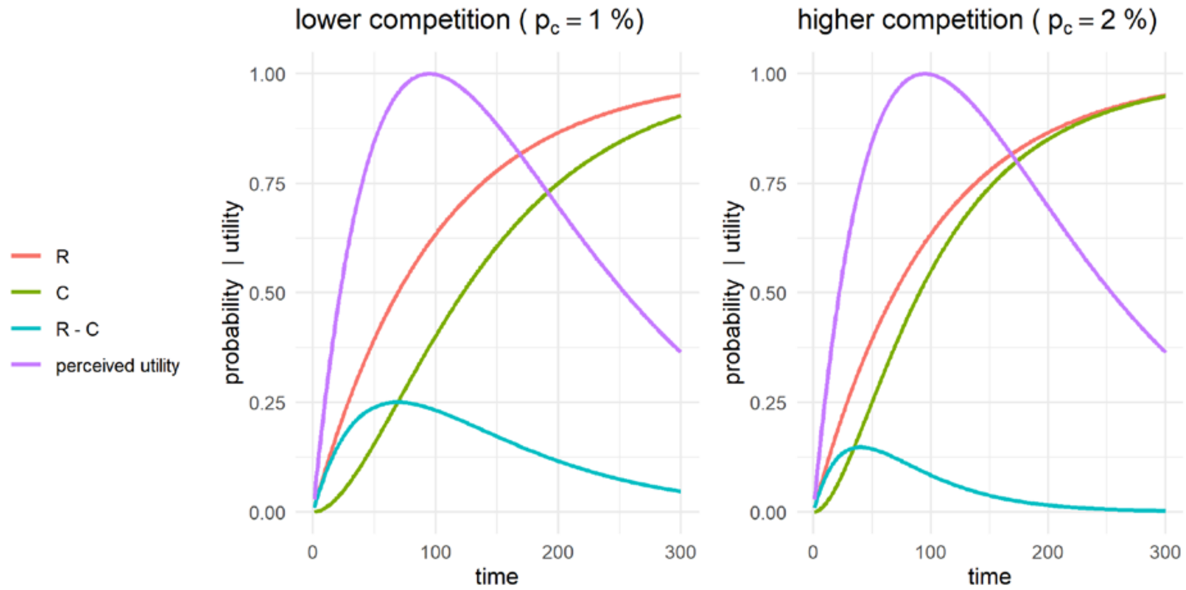


Figure 3 The perceived utility (divided by its maximum), the likelihood of growth (R), the likelihood that a competitor exploited the regrown resource first (C), at higher ($p_c = 0.02$) and lower ($p_c = 0.01$) levels of competiton (e.g. population density), and the differences between the likelihood of regrowth and likelihood of competition ($R - C$). For simplicity, we disregard that the likelihood of competition again alters the likelihood of regrowth.

We modified the calculation of reference and working memory given by van Moorter et al. (2009) by changing it from an iterative approach that requires a specification of the initial reference and working memory to a decay function that only requires the time since the resources were exploited from this patch as the determinant. The initial reference and working memory and the decay rates of van Moorter et al. (2009) can still be parameterized to give return a similar utility function (Fig. 5)

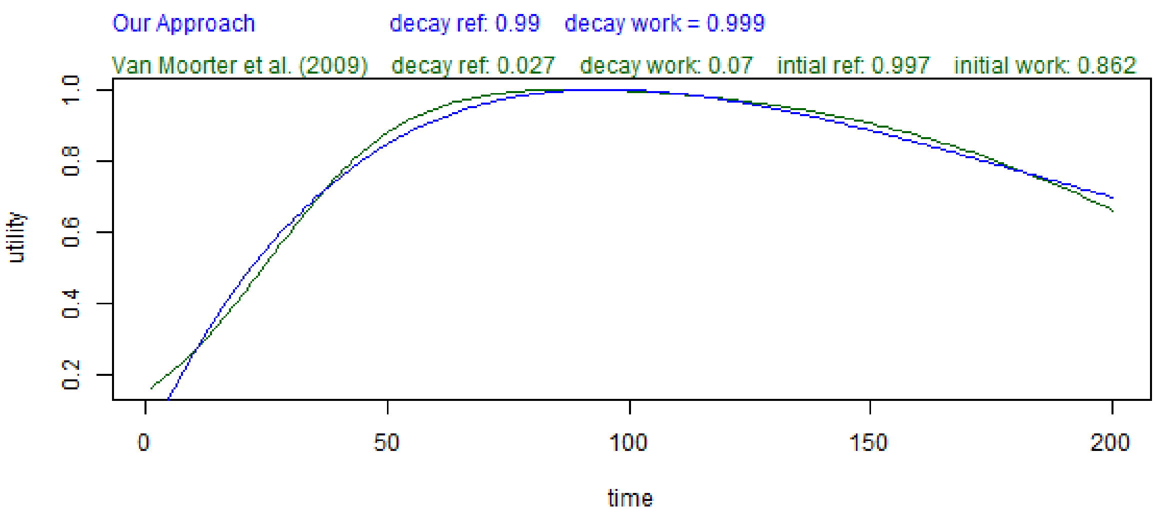


Figure 4 Changes in utility due to the two component memory over time in our approach and the approach by van Moorter et al. (2009) can yield similar results, if parameters are set accordingly. Note that the utilities of the different approaches in this example are divided by the maximum.

$$r(t_i) = \; {d_r}^{t_i}$$

$$w(t_i) = \; 1 - {d_w}^{t_i}$$

$$U_i = \frac{w(t_i) * r(t_i)}{|\overrightarrow{ap_i}|^2} \qquad (model\ equation\ I)$$

The mean attraction vector from memory is the sum of all vectors towards memorized patches converted to unit vectors $\frac{\overrightarrow{ap_i}}{|\overrightarrow{ap_i}|}$ and weighted by their utility U_i. To calculate the unit vector, the shortest path towards a memorized location $(\overrightarrow{ap})$ is determined …

Rationale: In a toroidal landscape there are multiple straight lines that connect two points, here the location of the animal a and the location of patch p. The shortest path is $\overrightarrow{ap}$.

… and divided by its length ($|\overrightarrow{ap}|$) and multiplied with U_i to combine utility and direction. The sum of

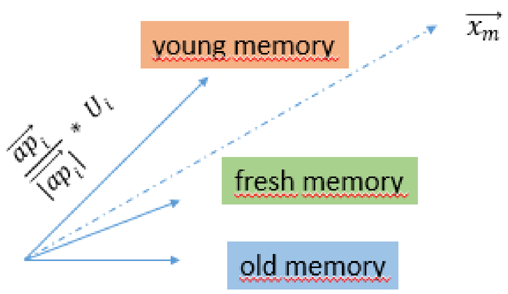


Figure 5 Example of the calculation of a mean attraction vector from memory. Opposing memorized patches would neutralize each other and therefore not contribute to the mean attraction vector.

all memory vectors is the attraction vector from memory $\overrightarrow{x_m}$.

$$\overrightarrow{x_m} = \sum_{i=1}^{n} \frac{\overrightarrow{ap_i}}{|\overrightarrow{ap_i}|} * U_i$$

In the model, the calculation of the equation above is split into 3 lines of code for the x and y component respectively:

- $\frac{\overrightarrow{ap_i}}{|\overrightarrow{ap_i}|}$ (model equation II),
- $\frac{\overrightarrow{ap_i}}{|\overrightarrow{ap_i}|} * U_i$ (model equation III),
- $\sum_{i=1}^{n} \frac{\overrightarrow{ap_i}}{|\overrightarrow{ap_i}|} * U_i$ (model equation IV).

Note that opposing vectors with equal utility would neutralize each other's effect on the mean attraction vector.

get-PoD

PoD (Persistence of Direction) defines the behavioural phenotype that depends on the environmental gradient (memory-feedback) and the behaviour type (alpha). The variable mem-feedback x is the 4th root of the length of the attraction vector from memory $|\overrightarrow{x_m}|$.

$$x = \sqrt[4]{|\overrightarrow{x_m}|} \qquad (model\ equation\ V)$$

Rationale: The length and direction of the attraction vector from memory results from the perceived utilities and the locations of the memorized patches. If there many patches are memorized, with high utility, memory-feedback is large and vice versa. Furthermore, if memorized patches with high utility are at a certain location instead of randomly distributed around the animal, the memory-feedback is higher as exactly opposing memorized patches neutralize each other and do not prolong the attraction vector. The directivity of the memorized patches affects the memory-feedback.

The transformation of the attraction vector from memory by the 4th root serves to adjust the emergent movement behaviour that results from the relationship between alpha and memory-feedback. Without the transformation, memory-feedback would be close to zero and PoD, hence, close to one. Linear transformation of the memory-feedback, e.g. by a factor of 10, leads to higher dynamics in PoD, but the movement pattern did not correspond to the desired central-place foraging. The transformation by the 4th root, however, facilitated central-place foraging without constraining the adaptive effect of the environmental gradient too much (e.g. demonstrated by larger home ranges in resource poor landscapes).

Now, the PoD (behavioural phenotype) is calculated via the behaviour type α and the <u>memory-feedback</u> as environmental gradient (Fig. 7).

$$PoD = 1 - \alpha * MemoryFeedback \qquad (model\ equation\ VI)$$

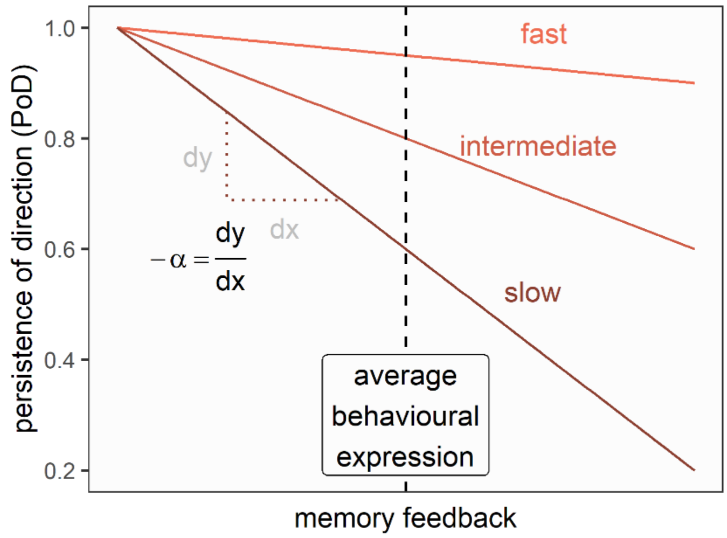


Figure 6 Linear behavioral reaction norm (BRN) with memory-feedback reflecting the environmental gradient and PoD as the behavioural phenotype. The behaviour type of an individual is defined by its α-level that regulates both, the responsiveness and the average behavioural expression. Larger α mean that individuals respond, in the PoD, stronger to both, the environment (memorized patches) and changes in the environment (caused by resource dynamics and competition).

Rationale: Animals should adapt their home ranging behaviour based on their expectations of the availability of resources. Behavioural changes require an environmental gradient to adapt to. In our model, the environmental gradient is defined by the perceived utility and location of memorized patches with resources. Utility and location constitute the length of the mean attraction towards memorized patches which is the determinant of the <u>mem-feedback</u>. The feedback is higher the higher the total perceived utility of all patches and the more uniform the direction towards the patches is. The higher the feedback the more an animal expects to gain benefits from returning to memorized patches. Therefore, a higher feedback is linked to a higher reliance on memory and, hence, lower PoD (details in section 7).

The higher the memory feedback and the higher α, the lower is PoD and the higher is the reliance on memory. For the sake of simplicity, the intercept at zero memory-feedback does not vary between individuals and is always 1. The correlation between mean behavioural response and responsiveness is based on existing evidence (Natarajan et al., 2009; Mazza et al., 2018).

If the PoD is below 0 it is set to 0.

Rationale: The PoD is fixed to a range of 0 to 1. Individuals with a PoD of 0 turn fully towards the mean attraction vector. Fixing the lower boundary to 0 is therefore necessary. However, drops of PoD to 0 have not been observed in test runs with individuals with an α-level of 1. A PoD of 0 becomes unlikely due to the underlying processes. The higher the PoD gets, the more likely it becomes that an individual will exploit a certain patch resetting the utility function (see. Fig. 3) or, if it is not successful at exploiting a patch, the utility will start to decrease.

set-new-heading-and-move

PoD and the attraction vector from memory ($\overrightarrow{x_m}$) determine the new mean attraction vector from memory ($\overrightarrow{\overline{x_n}}$). Hence, $\overrightarrow{\overline{x_n}}$ is a combination of the current movement direction $\overrightarrow{x_c}$ and the attraction vector from memory $\overrightarrow{x_m}$ weighted by PoD :

$$\overrightarrow{\overline{x_n}} = \mathrm{PoD} * \overrightarrow{x_c} + (1 - \mathrm{PoD}) * \overrightarrow{x_m} \qquad (model\ equation\ VII)$$

Finally, the direction of $\overrightarrow{\overline{x_n}}$ is slightly randomized by sampling from the van-Mises distribution with the radians of $\overrightarrow{\overline{x_n}}$ as its location parameter and κ = 10 as the scale parameter (Fig. 8). By moving one spatial unit towards this new direction, the decision-making is completed.

Rationale: The stochasticity induced by the van-Mises distribution should account for effects (i.e. disturbance, barriers) that may alter the movement path generated from memory and are not included in the model.

update-memory

After moving, the attributes of the current location (**patch**) are assessed. If <u>resource</u> on the current patch is 1 and it is not part of the **animal**'s <u>mem-patch</u> yet, the patch is added to the <u>mem-patch</u> list and gets a corresponding entry in <u>mem-time</u> of 0. If the patch is part of <u>mem-patch</u> already, the corresponding <u>mem-time</u> of the patch is reset to 0.

In any of these two cases, <u>resource</u> of the patch gets set to 0.

Rationale: Patches with <u>resource</u> 0 are not added to <u>mem-patch</u> as their perceived utility would be zero. Only patches with <u>resource</u> 1 affect the memory .

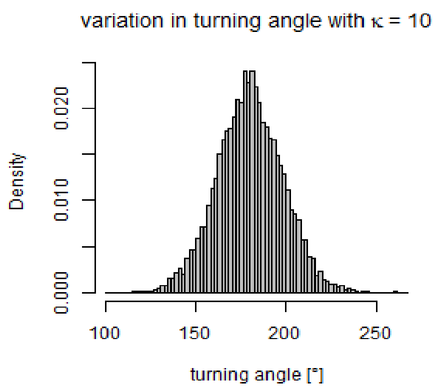


Figure 7 Sampled turning angles (n = 10,000) with the scale parameter κ = 10 and location parameter **π** (180°). **The location parameter is arbitrary as it depends on the direction of memorized patches**

Finally, all entries in <u>mem-time</u> are increased by 1 to account for the aging of the memory.

do-energetics

The submodel reduces mem-resources by 0.18 per time step and resembles maintenance costs.

Rationale: The maintenance costs of 0.18 per time step are derived from mean foraging efficiencies at the optimum of trait-foraging efficiency relationships in a patchy landscape.

If breeds is true, the animal increments breeding-stage by 1. The costs imposed on mem-resources (MR) per time step depend linearly on the breeding-stage (BS):

$$MR_{t+1} = MR_t - 0.0075 * BS$$

Rationale: The model's population dynamics are generically based on to the ecology of small mammals. To account for the increase in body mass during pregnancy and the increase in energy demand by the offspring during lactation, we assume a linear increase in the total energy demand.

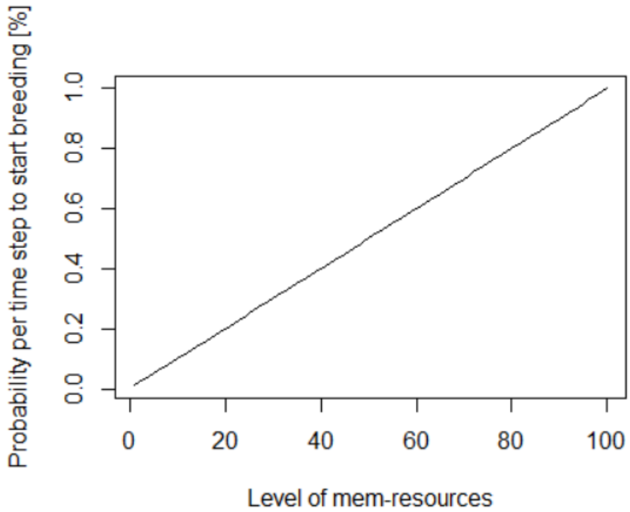


Figure 8 Probability per time step to attempt breeding in dependence of the level of mem-resources.

attempt-breeding

If breeds is false, the **attempt-breeding** sub-model is executed. Here, the animal attempts breeding whereas the likelihood to engage breeding depends on the level of mem-resources. The higher mem-resources, the more likely the animal will switch breeds to true (Fig. 9).

create-offspring

If the **breeding-stage** is at its maximum, the animal generates five offspring that share the same species-specific traits (species-mean, species-ID) and are assigned a value of alpha that is sampled from the species-specific uniform distribution defined by species-mean and ITV. The initial location is the same as the current parental location. All other state variables are set as during initialization of the model.

grow-resources

All patches with fertile 1 and resource 0 have 1%-chance to set resource back to 1.

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